

XVI. *Gynandromorphous Lepidoptera*. By E. A. COCKAYNE,  
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PLATES XCIII–CIV.

[Read October 4th, 1916.]

THE rarity of gynandromorphous Lepidoptera and the difficulty of obtaining them in a condition fit for dissection has stood in the way of the examination of their internal anatomy. The internal organs have been investigated and described in about twenty perfectly or almost perfectly halved examples. Eight of these in *Amorpha populi* I figured and described in the Journal of Genetics. Six of those previously described were also examples of gynandromorphs of this species. Since these were published I have dissected two more *Amorpha populi* and one *Amorpha hybridus* Steph. (*A. ocellatus* ♂ × *A. populi* ♀). As in the former examples the *populi* were from Newman's strain, as was the female parent of the hybrid. The hybrid was bred by Mr. Sydney Whicher, to whose generosity I am indebted for the specimen.

The first *A. populi* (R ♂, L ♀) showed in all external characters perfect halving, and the colour, dark grey, was the same on both sides. On dissection it proved to have on the right side a testis, vesicula seminalis, vas deferens, glandula accessoria, ductus ejaculatorius and penis, and on the left side an ovary with four follicles, oviduct, spermatheca or receptaculum seminis, cement gland, and bursa copulatrix. It was, in fact, a true genetic hermaphrodite without any reduplication of organs and with only one defect, absence of the ductus bursae or seminis. The external genitalia showed on the last segment a small uncus continuous in the usual way with the tegumen and cingula, and on the left a half ovipositor with its coarse tactile hairs and directing-rod. Opposed to the uncus was the gnathus, and between them lay the anus. The less distal segments showed a similar halved arrangement of male and female structures. There was a nearly perfect right valve (14) and harpe (15) and a much smaller left valve and harpe. Behind and between lay a normal ring-

wall (13) allowing the passage of a penis (7) narrower than usual but with well-formed oedaeagus, vesica and cornuti, the latter in two groups, a large group of large spines and a small group of small ones.

The tegumen and cingula (16), which in the normal male form a complete ring or girdle of stout chitin with a lateral hinge on each side, ended in the gynandromorph slightly to the left of the middle line. Thus on the male side all the parts were present, but the uncus and penis were small. The uncus is in reality a double organ, and in many groups is bifid. It is homologous with the two halves of the ovipositor.

The uncus was small because it was only half the ordinary double uncus, and I regard the narrowness of the penis as being due to the same cause. It was small because it was formed from only half the normal primitive epithelial mass of cells. There was reduplication of the clasping apparatus, valve and harpe, and partial reduplication of the cingula. On the left side was a small malformed bursa copulatrix and caput bursae, an abnormally small ostium bursae or genital opening and a normal rod of the ninth segment.

Thus the female parts were all present, but with the exception of the rod, a paired organ, all were small in size owing to their origin from half the usual number of epithelial cells.

The second gynandromorphous *A. populi* was not perfectly halved, the right side was predominantly female, and the left predominantly male. The wings on the left approached the female in shape, and the antenna on the left showed the coarse hairs peculiar to the male, though much less well-developed than those on the right. The colour, red brown, was the same on both sides.

Internally there was only one gonad, an ovary with four follicles, which lay on the right side of the body. There was also an oviduct, cement gland, spermatheca and very small bursa copulatrix and caput bursae, but no ductus seminis. On the male side there was only a penis with a soft saccular mass of chitin representing the blindly ending ductus ejaculatorius.

The external genitalia showed a completely halved arrangement. On the left side of the tenth segment was a small uncus and on the right a normal half ovipositor, with its directing-rod. Opposed to the uncus was a gnathus of small size, and between them lay the anal opening. On

the left were two valves and harpes rather compressed, the valve and harpe lying internally near the female organs being smaller and more distorted. There was a penis sheath, a narrow but perfect penis and a cingula, perfect on the left side but on the right very thin and soon ending by gradually disappearing in the thin chitin of the female side. On the right side was a small ostium bursae, from which ran a long thin tube, opening into a small twisted bursa copulatrix, with a small curved caput bursae. The directing-rod of the ninth segment was normal in size and shape.

The condition of the external genitalia in both gynandromorphs is the same in all important points.

The gynandromorphous hybrid was perfectly halved, being male on the right side and female on the left. The antenna and palpus of the right side showed perfectly developed male characters, those on the left female (Plate XCIV). The hair on the thorax and abdomen was longer and thicker on the right side, the division being accurately in the middle line. The abdomen was stouter on the left side.

The wings failed to expand, but those on the right side were darker and the basal patch of the hind-wing was larger and darker on the right side than the left. On both sides the characters were intermediate between those of the two parent species.

Internally the insect had no male organs, except the lower end of the ductus ejaculatorius, which formed a dilated sac opening into the penis, and there were no female organs except a bursa copulatrix of small size, and a cement gland of most abnormal shape.

The cement gland had a very narrow duct with an unusually large dilatation in its course, and the gland itself was double, one branch ending in a very small thin tubular part, the other in a tubular portion equally thin but longer, though not nearly as long as that of a normal gland. The duct ended in a mass of chitin near the neck of the bursa, and which probably represented the undeveloped vagina.

Thus, though the secondary sexual characters of both sexes were perfectly developed, the insect possessed neither ovary nor testis.

Externally the genitalia showed a perfectly halved condition, male on the right side and female on the left.

There was a small uncus and narrow sickle-shaped

gnathus enclosing the anal canal on the right side and a perfect half ovipositor and directing-rod on the left. A valve lay on the right side, distorted and possessing a curious prolongation of very thin chitin, with an up-curved, knob-like extremity. There was also a malformed harpe. A small piece of chitin (13) probably represented the ring-wall or penis sheath, and the penis itself was very short and was tilted so that the vesica pointed ventrally. The very small cornuti on the vesica resembled those of *ocellatus* rather than those of *populi*, a condition usual in male hybrids, in some of which no cornuti at all are present.

The cingula was present only on the right side, and ended abruptly in the mid-line. On the left side there was a thin, rounded piece of chitin external to the ovipositor, of the nature of which I am uncertain.

The ostium bursae was very small, and the bursa itself small and ill-formed. The rod of the ninth segment was normal.

The hybrid showed a perfectly halved condition of the external genitalia without reduplication or defect, and it is interesting that, although in the female hybrid male external organs are always found usually in the form of a coarse mosaic, none occur on the female half of this gynandromorph.

A comparison between the diagrams of the genitalia of the gynandromorphs, which are drawn partly as transparencies, with those of the genitalia of normal male and female *populi*, will make it easy to understand the exact degree of departure from the normal which the various structures in the gynandromorphs exhibit.

These three gynandromorphs, to my mind, are a further proof that the same underlying cause can produce true lateral genetic hermaphrodites, halved or lateral gynandromorphs with one or more gonads of one sex only, or without gonads of either sex, but with external structures of both sexes (primary somatic hermaphrodites).

The differences appear to me to be due to a failure of part of the genital tract to develop, a failure which is specially liable to affect the sexual gland itself.

With regard to the external genital organs, the ideal condition would be that in which exactly half the organs of each sex would be present. This cannot occur except in the case of the paired organs, such as the ovipositor and directing-rod, the rod of the ninth segment in the

female, and the valve and harpe in the male. In the case of these it is generally met with, but there is a tendency in the case of paired organs, which lie contiguous to one another, for the half-sized mass of epithelial cells, which theoretically should give rise to one full-sized member of a pair of paired organs, to produce actually an imperfect and undersized pair instead.

This occurs most often in the case of the valve and harpe in the male.

It does not occur in the case of the rod of the ninth segment, because the rods develop far apart, not close together, like the valves.

In the case of unpaired structures, especially those which are tubular or saccular, the half-sized mass of primitive cells gives rise to a complete tube or sac, which is reduced in size, and often imperfect in form.

Examples of this kind of structure are the penis in the male and the ostium bursae and bursa copulatrix in the female.

This explains the narrowness of the bursa and slenderness of the penis usually found in halved gynandromorphs.

Entire failure of a part to develop occurs less often in the external than in the internal organs, but in a genetic hermaphrodite, which I described and figured, the whole of the external genitalia of the female side failed to develop, whilst those on the male side showed reduplication.

They were, however, situated laterally on the male side of the insect and not centrally. Mr. Bethune Baker kindly called my attention to the account he published in these Transactions in 1891, of the external genitalia of a halved gynandromorph of *Eronia hippia* var. *gaea*. It is mounted laterally, and the point I wish to bring out is not clearly shown in his beautiful and accurate drawings. He has allowed me to examine the specimen, and I agree with all he says, except that what he regarded as combined valve and ovipositor I consider to be a valve lying over a half ovipositor. Examination of it from above and below with careful focussing has convinced me that the specimen agrees with the majority of gynandromorphs of this kind, and that the arrangement of the parts is that shown in my diagrams (Plates CIII and CIV). On the left side of the terminal segment one can see a half ovipositor with its rod, on the right a narrow uncus, from which runs as a half girdle the tegumen and cingula. The saccus, a structure not

present in *Amorpha*, is very narrow, being another example of an unpaired organ reduced in size because it is developed from half the usual number of cells. From the other side of the saccus runs a small piece of cingula, an example of partial reduplication of what is really a paired structure, which, like the uncus, has become fused. Two valves are present, though not quite normal in shape, and the penis is more slender than usual. The female half is the more interesting.

In the normal *gaea* there is a most elaborate ostium bursae, guarded by two folds of chitin, covered with coarse, curved hairs, and in the ventral wall of the bursa itself is a dense mass of chitin with two wings covered with short, thick spines, a structure corresponding to the signum of the geometrid bursa.

In the gynandromorph the ostium has only one of the chitinous folds present, that lying on the left or female side.

The whole bursa is small in size, and only the left wing of the signum is present (Pl. CIV).

This is the best proof I have met with that the small bursa of the gynandromorph represents a half bursa. The primitive cell mass, half the usual size, could complete the tubular neck and saccular body of the organ, but could not develop more than one half of such an elaborate structure as the chitinous fold guarding the ostium or the signum in *gaea*.

#### THEORY OF ORIGIN OF HALVED GYNANDROMORPHS.

When I published my paper in the Journal of Genetics in 1915 I was unaware of the earlier writings of Morgan on this subject. In his first paper, published in 1905, "An alternative interpretation of Gynandromorphous Insects," he suggests that two spermatozoa may enter the same egg, and that one of these develops without any fusion of its nucleus with the nucleus of the egg, whereas the other fuses in the usual way. The independently developing spermatozoon derived solely from the male parent produces the male part of the perfect insect. The other, combined with the ovum, produces the female part, which is thus derived from both parents.

The theory is alternative to that put forward by Boveri, who thought that there was a premature division of the egg nucleus, one half of which combined with the whole

nucleus of a single spermatozoon and gave rise to the male portion of the gynandromorph, the other half developed parthenogenetically and gave rise to the female portion.

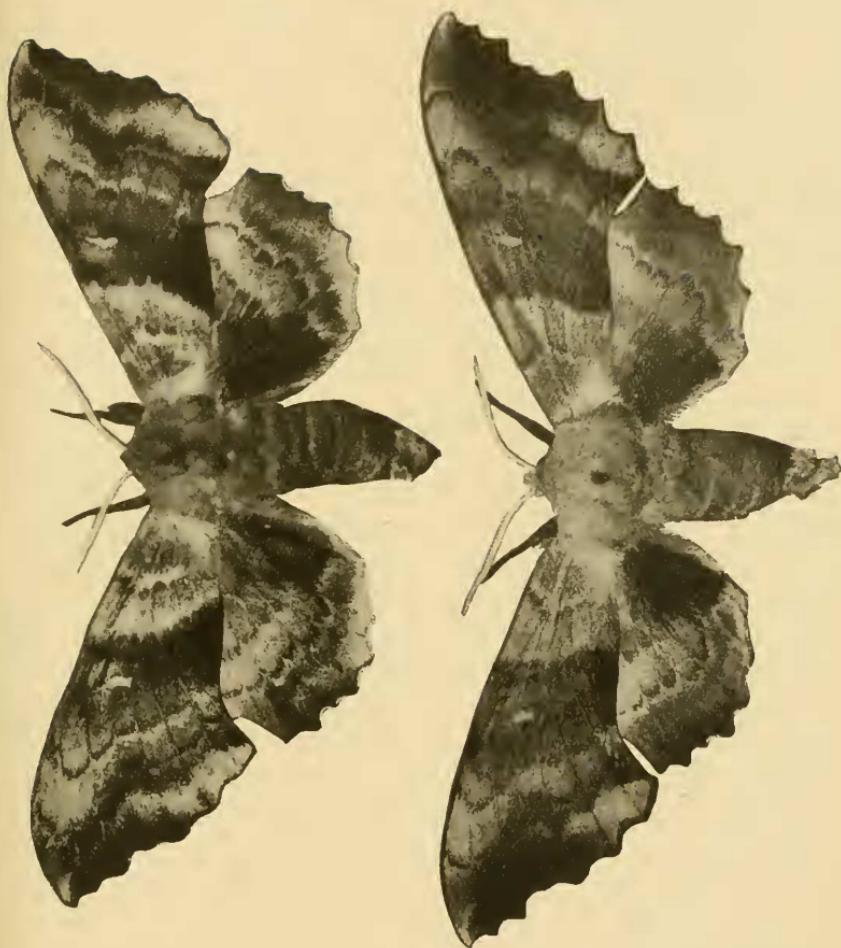
In his second paper, in 1907, Morgan reiterated his theory, and in support of it brought forward Toyama's gynandromorphous *Bombyx mori*.

The larva of this insect was striped on the left side, and the imago was female on this side; the right side of the larva was plain and of the imago, male. The striped condition of the larva is a Mendelian dominant over the plain. Morgan regards the striped female half as being derived from the combination of a spermatozoon carrying the recessive "plain" character with an ovum carrying the dominant "striped" character, and the plain male half as being formed from another spermatozoon, which entered the egg and developed without any fusion with the nuclear substance of the egg.

Boveri's hypothesis rests on the condition met with in the gynandromorphs of the Eugster hive of bees. In these insects Newell has shown by the following experiments that drones inherit the characters of the queen. An Italian yellow queen crossed with a Carniolian grey drone produced yellow workers and queens, and the drones were yellow also. A Carniolian grey queen and an Italian yellow drone produced yellow workers and queens, but the drones were grey. This shows that yellow is dominant over grey, and that drones are produced from unfertilised eggs, and derive their characters from the queen or female parent only.

Boveri carefully examined some of the Eugster gynandromorphs preserved in spirit, and in spite of the loss of colour he made out that the male parts were maternal and the female parts paternal in their characters. The colour of the male parent was dominant over the colour of the female parent.

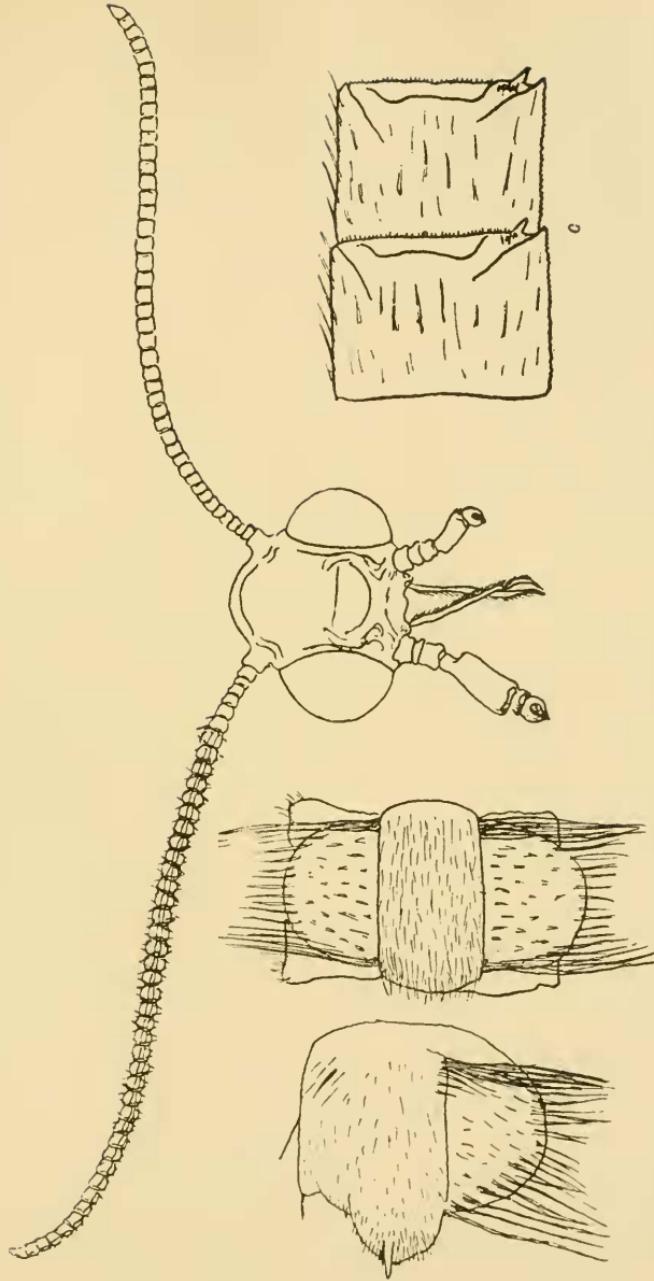
Mehling made an independent examination of the material and arrived at the same conclusion. The condition found in these bees supports the view that the male parts are derived from the unfertilised part of the ovum, the female from the fertilised part. Another hive of bees has recently been met with at Terek-Gebiet in the Northern Caucasus, and has produced many gynandromorphs, some of which are halved. They were the offspring of an Italian queen by an unknown drone, probably of the form known as *Apis mellifica remipes*. These gynandromorphs, according



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*Gynandromorphous Amorpha populi.*





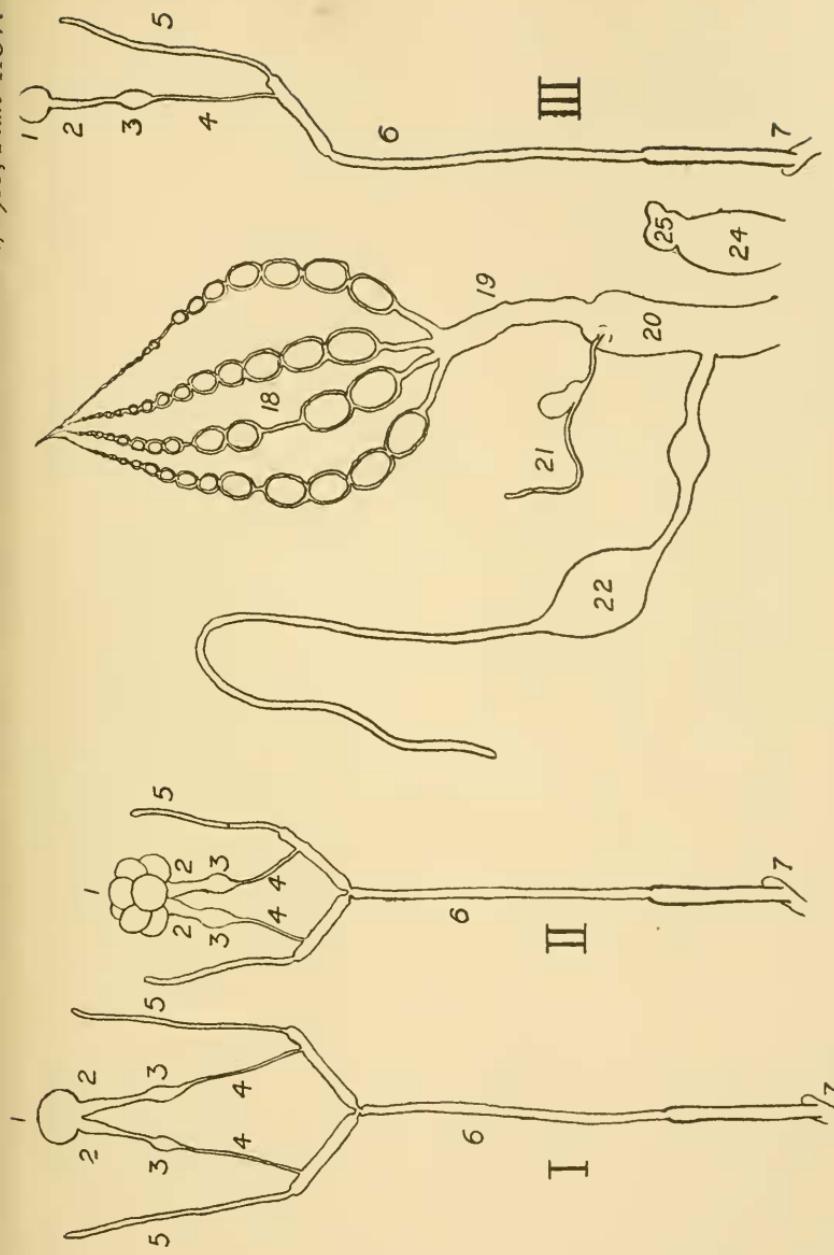
*E. A. Cockayne, del.*

*b*

*Head of gynandromorphous *Amorpha hybridus*.*

*c*

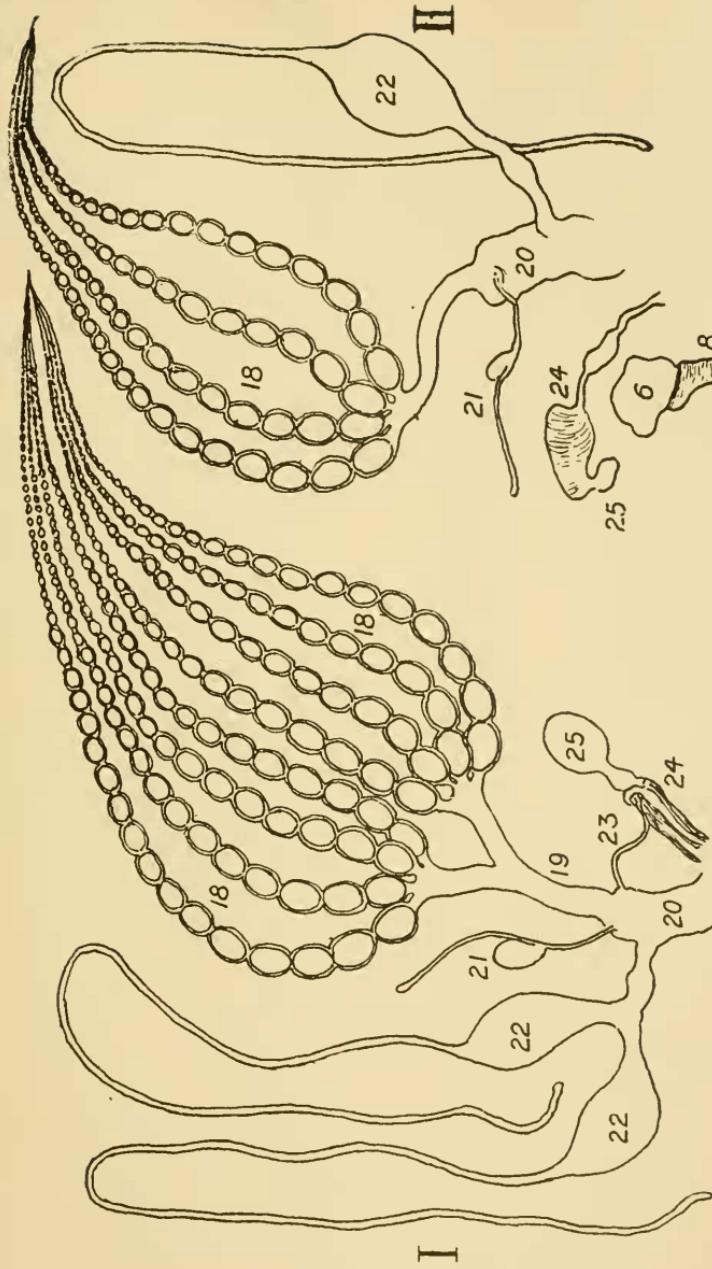




E. A. Cockayne, del.

Internal genitalia of (I) Normal male, (II) Intersex, (III) gynandromorphous *Amorpha populi*.





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Internal genitalia of (I) Normal female, (II) gynandromorphous *Amorpha populi*.